ON THE GENERIC STATUS OF *PALAEOPHICHTHYS PARVULUS* EASTMAN 1908 AND *MONONGAHELA STENODONTA* LUND 1970 (OSTEICHTHYES: DIPNOI)

ANNE KEMP[1]

ABSTRACT

The genus *Monongahela* Lund 1970, a species of dipnoan based on small tooth plates from the Duquesne limestone, Upper Pennsylvanian, in Mount Washington, Allegheny County, Pennsylvania, has been designated a junior synonym of *Palaeophichthys parvulus* Eastman 1908. Alternative interpretations of the material are, however, possible. *Palaeophichthys parvulus* is known from two juvenile specimens from the Francis Creek shale, Carbondale Formation, Middle Pennsylvanian, in the Mazon Creek area of Grundy County, Illinois. These are compressed, with macerated heads. The holotype has poorly preserved upper and lower tooth plates. Characters for comparison with *Monongahela* can be derived only from the upper tooth plates. None of the tooth plate characters that can be reliably distinguished in *P. parvulus* are sufficient to separate this species from a range of other lungfish genera, and both taxa are found at localities where other dipnoan genera occur. Because additional material and definition of all of the lungfish in the localities are needed to settle the question of congenerity of *Palaeophichthys* and *Monongahela,* separation of the two genera should be retained at present.

KEY WORDS: fish, *Palaeophichthys*, *Monongahela*, Carboniferous, Dipnoi

INTRODUCTION

Palaeophichthys parvulus is a problematic dipnoan taxon, described by Eastman (1908) on a small, poorly preserved specimen. A second specimen, slightly larger, was assigned to this species later (Eastman, 1917), but this material adds little information. Both specimens are compressed and have reasonable preservation of the body form and the squamation, but the heads are macerated. *Monongahela stenodonta,* described by Lund (1970), is a genus based on an extensive series of small tooth plates and jaw bones from a slightly younger locality. No skull bones or compressed fish are known for this genus. *Monongahela* has recently been made a junior synonym of *Palaeophichthys* (Schultze, 1994), an opinion based apparently on the existence in the holotype of *P. parvulus* of a single, partially preserved upper tooth plate that resembles the tooth plates described as *M. stenodonta*. Schultze (1994) has further described *P. parvulus* as a gnathorhizid, despite characterizing the skull roof as having a series of unpaired median bones.

Comparison of the two specimens of *P. parvulus* with tooth plates and body form in hatchlings of one species of a Recent lungfish, *Neoceratodus forsteri,* suggests that both specimens of *P. parvulus* are juvenile, as are the tooth plates belonging to *M. stenodonta.* Diagnosis of species on juvenile material is possible in a bradytelic group like lungfish, but none of the characters used by Schultze (1994) are reliable at generic or specific level. Consideration of both specimens of *P. parvulus* and comparison of the upper tooth plates with material from other

genera, including specimens of *Sagenodus* cf. *S. periprion,* contemporaneous with *M. stenodonta,* suggests that synonymy is premature. Examination of available characters indicates that although *Palaeophichthys* and *Monongahela* are not congeneric, it is impossible at this stage to be sure of the true affinities of *P. parvulus.*

Specimen designations: CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachussetts; QM, Queensland Museum, South Brisbane, Queensland, Australia; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D. C.

MATERIALS AND METHODS

Comparable Populations of Juvenile Dipnoans

A large sample of young *Neoceratodus forsteri,* collected as eggs from the Brisbane River in southeast Queensland and reared in the laboratory, including juvenile fish of stages 53–57 and isolated tooth plates of stages 54–57, has been used for comparison with the holotype and the hypotype of *P. parvulus* and with other fossil material. Stage 53 hatchlings are three months old and stage 57 hatchlings are nine months old. Growth and development of young stages of *N. forsteri* is described in Kemp (1982), and additional details are provided in the description below. Tooth plates and attached jaws of *M. stenodonta* came from the type locality of the Duquesne limestone (Lund, 1970). Additional juvenile specimens of *Sagenodus* cf. *S. periprion* from the same locality as *M. stenodonta* were used for an outgroup comparison. Specimens of this taxon provide the only possible outgroup comparison, not because they are necessarily appropriate in cladistic terms, but because this population is the only other large sample of juvenile fossil dipnoans that are less derived than *Monongahela* and *Palaeophichthys.*

Originals of the holotype and hypotype of *P. parvulus* have been examined in the National Museum of Natural History, Smithsonian Institution, Washington, D. C., and in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, and compared with latex peels of the same specimens in the personal laboratory of Dr. D. Baird, Pittsburgh, Pennsylvania, and at the Museum of Natural History, University of Kansas at Lawrence. The holotype of *M. stenodonta* has been examined at Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, and a series of specimens were borrowed for more detailed comparison and analysis.

Scanning Electron Microscopy

Isolated tooth plates were mounted on stubs, coated in gold, and examined in a Phillips 505 scanning electron microscope.

Biometry

Measurements of lengths and breadths of the tooth plates and of the angles between the ridges were done by making a camera lucida drawing of the occlusal surface of each tooth plate, set level, and measuring angles and lengths on the drawing with a ruler and protractor. The enlargements of each specimen were the same in every case. Positions of the measurements of lengths, breadths, and angles taken are shown in Figure 1. Length of the tooth plate from the tip of ridge 1 to the tip of the last ridge is the dimension most suitable for tooth plates that are
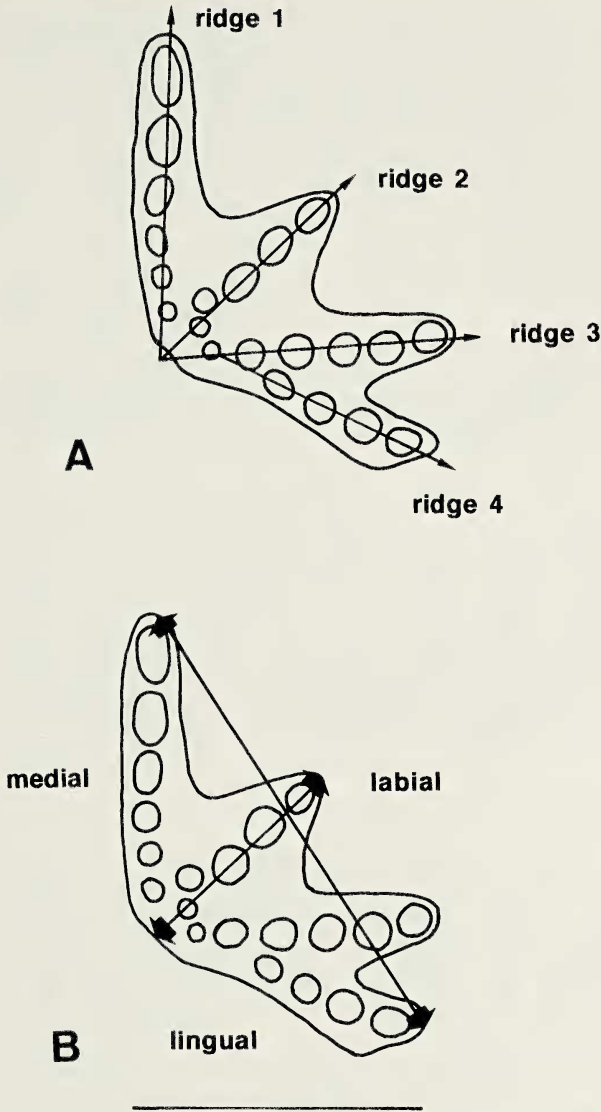
Fig. 1.—Measurements taken of tooth plates based on an upper tooth plate of *Neoceratodus forsteri* at stage 54, and terms used when describing tooth plates. A, angles between ridges; B, length and breadth. Scale bar = 1 mm.

still cusped. Breadth of the tooth plate is taken from the mediolingual junction to the tip of ridge 2. Angle measurements were done by fitting a straight line as closely as possible to the midpoints of each cusp. The ridges rarely meet in a point if the angles are drawn in this way, and further problems arise if the ridge is curved. However, the angles obtained for *M. stenodonta* are consistent with those obtained by Lund (1970, 1973), who used a different method.

Angles between the ridges of the upper tooth plate of *P. parvulus* are taken from Schultze (1994) and were also measured on his scanning electron micrograph
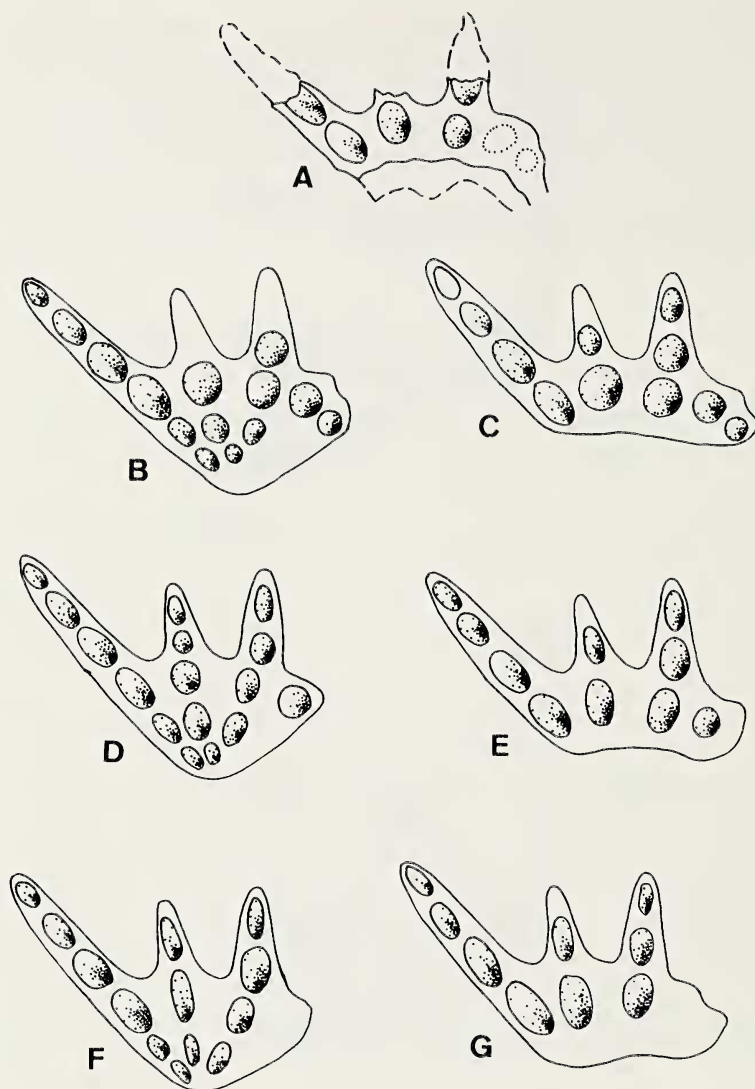
Fig. 2.—Drawings of the left pterygopalatine tooth plate of the holotype of *Palaeophichthys parvulus*. A, actual tooth plate drawn from the scan in Schultze (1994) and from latex peels; B, C, tooth plate reconstructed with five ridges; D, E, tooth plate reconstructed with four ridges; F, G, tooth plate reconstructed with three ridges. B, D, and F have ridges meeting in a point, with the medial portion of the tooth plate reconstructed. C, E, and G have no medial portion, and the tooth plates radiate from a line. Scale bar = 1 mm.

of the latex peel of the specimen (Fig. 2). Because measurements made on scanning electron micrographs require extensive correction before they can be accepted as accurate, these measurements of angles of *P. parvulus* are of value for descriptive purposes only.

Measurements of the lengths of the body and head of living *N. forsteri* hatch-

Table 1.—*Characters used to determine the biological age of the specimens. 1 = squamation; 2 = calvarial bone development; 3 = articulation, calvarial bones; 4 = enamel cover; 5 = severity of wear on cusps; 6 = development of secondary denteons. See text for details.*

Genus	Character					
	1	2	3	4	5	6
Neoceratodus stage 53	full	early	none	full	slight	none
Neoceratodus stage 55	full	partial	partial	full	slight	none
Monongahela	?	?	?	full	slight	none
Palaeophichthys	full	partial	partial	full	slight	none
Sagenodus	?	?	?	full	slight	none

lings, and the depth of head, body, and tail fin were done using calipers on anesthetized specimens. Measurements of the head and body of *P. parvulus* are taken from Schultze (1994).

Determination of the Biological Age of the Material

Biological age of a fossil specimen at death can be deduced from a number of characters by comparison with the juvenile, laboratory-reared material of known age from *N. forsteri.* Characters used to determine the age of the fossil species are squamation, degree of development and of articulation of the skull bones, enamel cover of the cusps, amount of wear on the cusps of the tooth plate, and the number of secondary denteons developed between the primary ridges. In the juvenile material of *N. forsteri,* these characters can be defined in full (Table 1). Only some can be determined for the fossil material.

Characters for Taxonomic Separation of Juvenile Dipnoans

Characters are modified from the lists used for adult lungfish in Kemp (1991*a*, 1992*a*, 1993*a*) and the characters used by Lund (1970, 1973). Some characters used on adult tooth plates and jaw bones were of no value for juveniles, as they have not yet developed, and others were too variable in young material. *Sagenodus* was used as the outgroup comparison. Characters are listed in the Appendix and explained below. The characters chosen apply for generic separation only, as *Palaeophichthys* is monotypic.

Character 1.—Shape of the upper symphysis is linear in *Sagenodus.* Other shapes, usually oval or half oval, are regarded as derived.

Character 2.—Shape of the lower symphysis is oval in *Sagenodus,* and other shapes, usually linear, are derived.

Character 3.—*Sagenodus* lacks an ascending pterygopalatine process for articulation with the dermal skull roof, but a process of variable shape is present on the pterygopalatine bone in the other genera examined.

Character 4.—Petrodentine, as defined by Lison (1941), is not common in dipnoans (Kemp, 1991*b*, 1992*b*; Lund et al., 1992). Absence of blocks of petrodentine in the tooth plates of juvenile lungfish is primitive, and its presence is derived (Kemp, 1995*a*). Small quantities of petrodentine may develop in older tooth plates of *Sagenodus* species, but this hard tissue is absent in juvenile *Sagenodus.*

Characters 5, 6, 7, and 8.—Shapes of ridge 1 and of the posterior ridges in each jaw are considered separately because they are not always the same. In the

upper tooth plate, curved ridges are primitive, and straight are derived. In the lower tooth plate, straight ridges are primitive, and curved ridges derived.

Characters 9, 10, and 11.—Most cusps in lungfish tooth plates show some compression, and this is often greater in the first ridge of a tooth plate compared to more posterior ridges. Compression is also more obvious in lower tooth plates. Slight lateral compression is regarded as primitive, and strong compression as derived.

Characters 12 and 13.—Ridge numbers in both upper and lower tooth plates vary according to growth and also show inherent variation. This character is often the same across a wide range of dipnoan genera, and to be useful, it must be defined with care. Juvenile tooth plates with more than five ridges in the upper jaw and more than four in the lower are primitive, and tooth plates with five ridges or less in the upper and four ridges or less in the lower are derived. This compromise applies only to juveniles in the genera considered here. Adult *N. forsteri* tooth plates have five or more ridges in both upper and lower jaws. Adult *Gnathorhiza* tooth plates have four ridges in the upper jaw and three in the lower. *Sagenodus periprion* has numerous ridges in each adult jaw.

Character 14.—Ridge 4 in the upper tooth plate, when present, may show the primitive condition, and begin level with ridge 3, at the mediolingual face, or start half way down ridge 3, independent of the mediolingual face. The latter character state is derived.

Characters 15 and 16.—In primitive dipnoans, the prearticular or pterygopalatine bone below the tooth plate extends beyond the dental tissues. In derived dipnoans, it follows the contours of the attached tooth plate.

Characters 17 and 18.—In primitive tooth plates, the ridges originate from a mediolingual line or curve. In derived specimens, the ridges of juvenile dipnoans originate approximately from a point situated medially or mediolingually.

SYSTEMATIC PALEONTOLOGY

Subclass Dipnoi Muller 1845
Family incertae sedis
Genus *Palaeophichthys* Eastman 1908
Synonym: None

Palaeophichthys Eastman, 1908:253, fig. 37.
Palaeophichthys Eastman, 1917:272, pl. 10, fig. 2.
Palaeophichthys Schevill, 1932:85.
Palaeophichthys Vorobyeva and Obruchev, 1964:314.
Palaeophichthys Romer, 1966:362.
Palaeophichthys Jessen, 1973:177.
Palaeophichthys Bardack, 1979:511.
Palaeophichthys Carroll, 1988:612.
Palaeophichthys Maples and Schultze, 1989:257, table 1.
Palaeophichthys Schultze, 1992:200.
Monongahela Schultze, 1992:201.
Palaeophichthys Schultze and Marshall, 1993:212.
Palaeophichthys Schultze, 1994:106–107.
Monongahela Schultze, 1994:107.

Amended Diagnosis.—Dipnoan with gracile and elongate body form; head short in relation to body; scales elongate, parallel sided, longitudinally striated with short, vermiculated free field; pterygopalatine tooth plate having straight radiating ridges with strong lateral compression of the cusps in the first ridge and

slight compression of the cusps in the second and subsequent ridges; prearticular tooth plate indeterminate.

Range.—Westphalian D, Upper Carboniferous.

Type Species.—*Palaeophichthys parvulus* Eastman 1908.

Palaeophichthys parvulus Eastman 1908

Palaeophichthys parvulus Eastman, 1908:253, fig. 37.
Palaeophichthys parvulus Eastman, 1917:272, pl.10, fig 2.
Palaeophichthys parvulus Schevill, 1932:85.
Palaeophichthys parvulus Vorobyeva and Obruchev, 1964:314.
Palaeophichthys parvulus Jessen, 1973:177.
Palaeophichthys parvulus Schultze, 1994:107.

Diagnosis.—As for genus.

Stratigraphic Position and Locality.—Francis Creek shale, Carbondale Formation, Middle Pennsylvanian (Westphalian D); Mazon Creek area, Grundy County, Illinois, USA.

Holotype.—MCZ 5090a, b, compressed fish with macerated head.

Hypotype.—USNM 4433, compressed fish with severely damaged head region.

Description.—*Palaeophichthys parvulus* is a dipnoan of slender and elongate shape. The head appears to be short in relation to the length of the body (14–15%) in both specimens, but because the full extent of the fleshy operculum is not preserved, the head may have been longer in the living fish. The tail is diphycercal, and the squamation well defined. The dentition is poorly preserved, and the only useful dental characters come from the pterygopalatine tooth plates. The right is represented by a lateral view of the first ridge only. The left appears to have three, four, or possibly five straight radiating ridges with strong lateral compression of the cusps in the first ridge and slight compression of the cusps in the second and subsequent ridges (Fig. 2A). Depending on the particular reconstruction used (Fig. 2B–G), ridge 4 may begin halfway down ridge 3, or may originate, like the other ridges, from a medial line or curve (Fig. 2B–G). The lower jaw is undiagnostic in both specimens. Despite the poor preservation, it is possible that there are three ridges in the prearticular tooth plate, but this is found in so many dipnoans, juvenile and adult, that it cannot be used for taxonomic determination. The fragment labelled as a vomer in Schultze (1994) has no characteristics of a vomer in the original specimen. It is present only as an impression, and alternative interpretations of this fragment are more probable, perhaps as one of the unidentifiable pieces of scattered and macerated skull bone.

In the holotype, the right pterygopalatine tooth plate is represented by three sharp, laterally flattened cusps of the first ridge, still covered to the tip in shiny brown enamel. No other ridges are visible. This appearance is consistent with any one of the species of small dipnoan contemporaneous with *Palaeophichthys* or *Monongahela.*

The left pterygopalatine tooth plate is represented by an impression, shown as a positive scan by Schultze (1994). Aside from the poor preservation, the mediolingual junction of the tooth plate is missing, as are the labial extremities of all the ridges. Traces of three ridges are present, as well as a probable fourth and a possible fifth (Fig. 2). Schultze (1994) has provided only one of several potential interpretations, and the characters displayed by the specimen are not entirely consistent with those of other dipnoan genera, even *Monongahela.*

One possibility is that five ridges are present (Fig. 2B, C). Ridge 1 has flattened cusps, ridges 2 and 3 have rounded cusps, ridge 4, with two rounded cusps begins in the middle of ridge 3, and ridge 5, with one cusp, has just begun to grow. It is possible that the ridges are long, straight, and acute, and radiate from a medial or posteromedial position (Fig. 2B). Alternatively, the ridges may radiate from a line or curve and may be short (Fig. 2C). The tooth plate may have only four ridges, the first long and straight with laterally flattened cusps, and the subsequent ridges shorter and also straight but with rounded cusps (Fig. 2D, E). The fourth may have begun to grow midway down ridge 3 (Fig. 2D), or all four ridges may radiate from a line or curve (Fig. 2E). It is also possible that only three long, straight ridges are present, radiating from a medial or posteromedial position, with the first long and straight with laterally flattened cusps, and the subsequent ridges shorter and also straight but with rounded cusps (Fig. 2F), or shorter, and radiating from a line or curve (Fig. 2G).

Comments.—Specimens of *Neoceratodus forsteri,* comparable in size with

Fig. 3.—Living hatchling of *Neoceratodus forsteri.* Scale bar = 1 cm.

those of *P. parvulus* (Fig. 3), are also slender and elongate. The head is long relative to the length of the body, 26–27%, but in the living juveniles considered for this paper, the head was measured to the back of the operculum, largely a fleshy structure in *N. forsteri.* The measurement of the head is, therefore, not strictly comparable in the two species. The pterygopalatine tooth plates that are commensurate in size with the tooth plate of *P. parvulus* have four straight ridges, with cusps in all ridges showing some slight lateral compression. In most upper tooth plates, ridge 4 begins midway down ridge 3 (Fig. 4A). Lower tooth plates are similar but have only three ridges at this age (Fig. 4B).

Comparable characters with the ability to discriminate generic status in *M. stenodonta* are the four radiating ridges in the pterygopalatine tooth plate, the first straight and the second and subsequent curved, all having cusps that are strongly compressed laterally (Fig. 4C, D). Cusps of ridge 4 begin to form midway down ridge 3. Lower tooth plates are similar, but have only three ridges. Characters of the body and head of this genus are not known. Vomerine teeth, however, have numerous small cusps (Lund, 1970).

Specimens of *Sagenodus* cf. *S. periprion* from the Duquesne limestones are known only from a number of upper and lower tooth plates with attached pterygopalatine and prearticular bones, all a little larger than *P. parvulus.* Pterygopalatine tooth plates have six or more curved ridges (Fig. 4E), and prearticular tooth plates have five or more straight ridges (Fig. 4F). Cusps of the first ridges show slight compression in both upper and lower tooth plates, and are short, rounded cones in the subsequent ridges, with the newest-formed cusp showing slight lateral compression (Fig. 4E, F).

In *N. forsteri, M. stenodonta,* and *P. parvulus,* ridges radiate roughly from a mediolingual point, and the angles are wide (Fig. 4, Appendix). In *S.* cf. *S. periprion,* angles are small, and the ridges radiate from a mediolingual line or curve (Fig. 4, Appendix).

Biological Age of the Specimens.—Characters for the assessment of the biological age of the specimens are listed in Table 1. Measurements of the head, tail, and body of *N. forsteri* juveniles, stages 53–57 (Kemp, 1982), are illustrated graphically in Figure 5, and mean angles between the ridges of upper and lower tooth plates are listed in Table 2. Corresponding available measurements of the angles between the ridges of *M. stenodonta* and *Sagenodus* cf. *S. periprion* specimens, as well as angles between the ridges of *P. parvulus,* are included in the
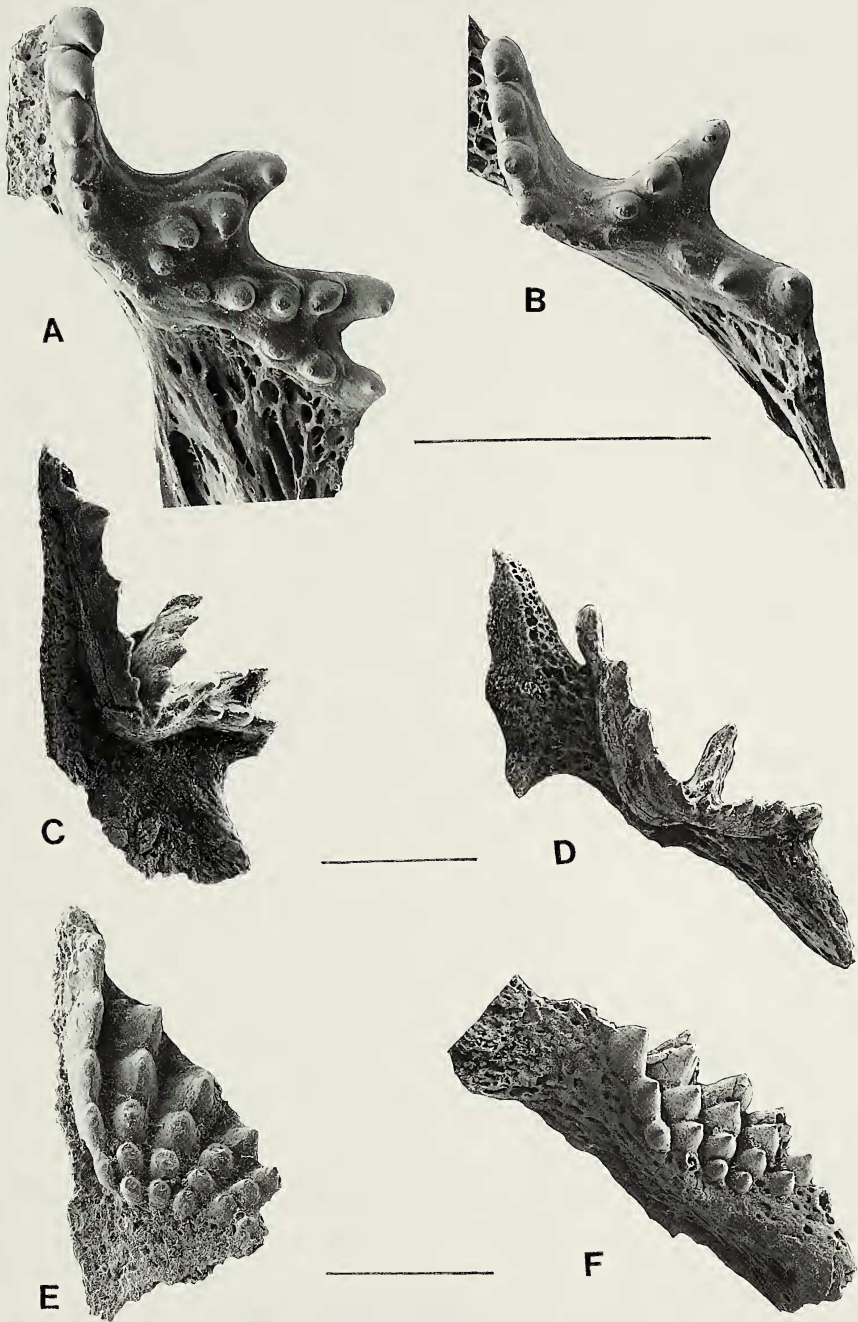
Fig. 4.—Scanning electron micrographs of juvenile lungfish tooth plates. A, B, *Neoceratodus forsteri.* A, upper tooth plate QM 26023; B, lower tooth plate, QM 26024. C, D, *Monongahela stenodonta.* C, upper tooth plate, CM 25633; D, lower tooth plate, CM 19415. E, F, *Sagenodus* cf. *S. periprion,* CM collection. E, upper tooth plate; F, lower tooth plate. Scale bars = 1 mm.
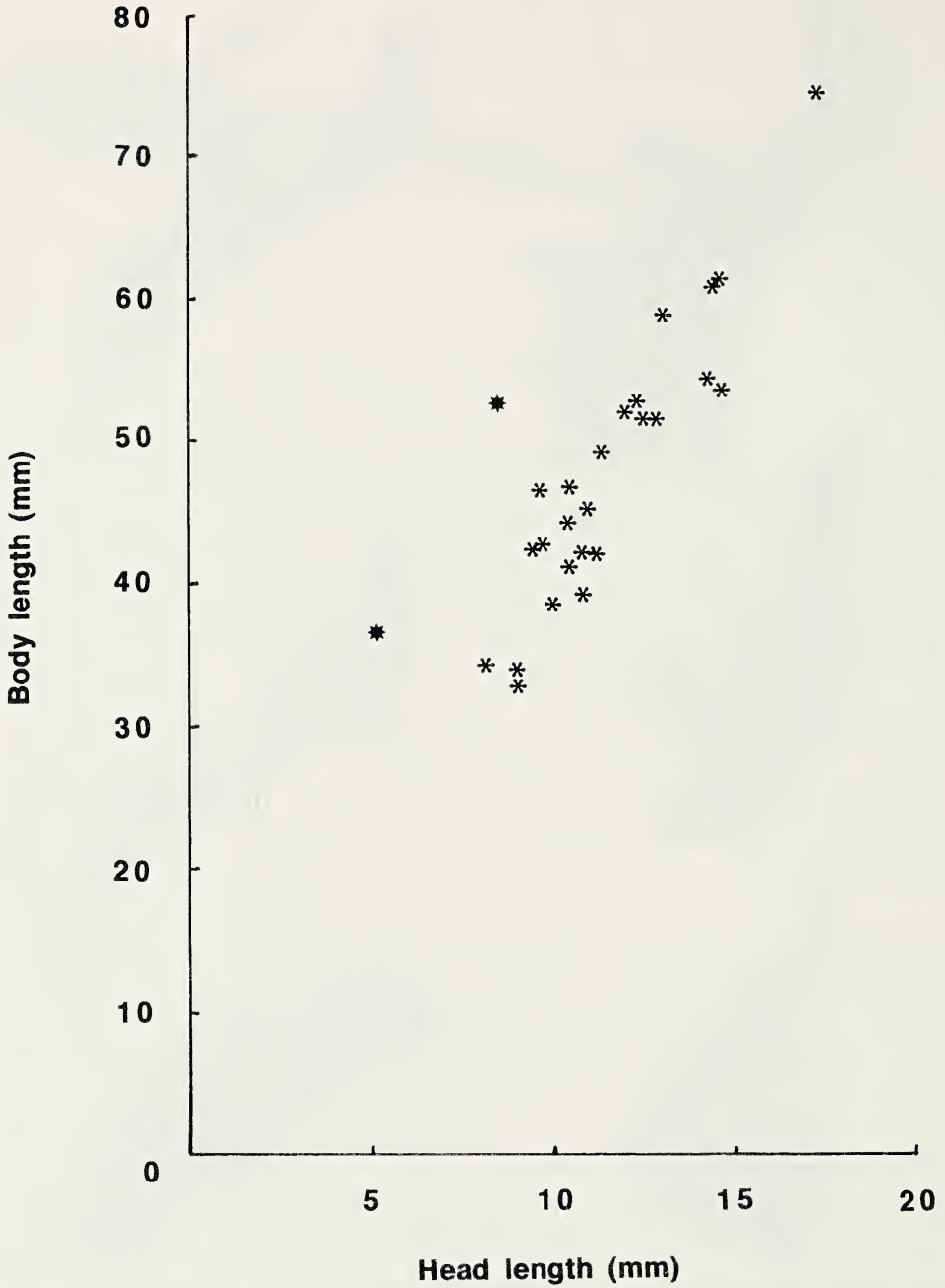
Fig. 5.—Graph showing body lengths of *N. forsteri,* with the sizes of *P. parvulus* material included. Asterisks represent the data for *N. forsteri* hatchlings, and stars the data for *P. parvulus* hatchlings.

Table 2.—*Measurements of upper tooth plates of dipnoan species.*

	Length	Angle, ridges 1–2	Angle, ridges 2–3	Angle, ridges 3–4	Angle, ridges 4–5
Neoceratodus forsteri	1.5 mm ± 0.3 mm	51.6° ± 5.6°	35.7° ± 5.0°	24.7° ± 6.34°	—
Monongahela stenodonta	2.6 mm ± 1.2 mm	40.4° ± 6.5°	40.2° ± 8.5°	31.2° ± 8.3°	—
Sagenodus cf. *S. periprion*	2.6 mm ± 1.2 mm	10.7° ± 2.9°	16.2° ± 5.1°	14.7° ± 5.7°	20.2° ± 5.1°
Palaeophichthys parvulus	1.2 mm[1]	40°[1]	28°[1]		
	1.2 mm[2]	35°	24°	30°	23°

[1] From Schultze, 1994.
[2] Specimen incomplete, but would have been larger than 1.2 mm.

table. Relative dimensions of the body and head of *P. parvulus* are indicated in Figure 5.

Although the head of *P. parvulus* is apparently shorter in relation to the body compared with juvenile *N. forsteri,* the body form of both species is elongate. *Palaeophichthys parvulus* is more gracile than *N. forsteri,* but both specimens fit within the range of body lengths of *N. forsteri* juveniles (Fig. 5), with the holotype closest to stage 53 of *N. forsteri* and the hypotype closest to stage 55 (Fig. 5). The holotype of *P. parvulus* is 3.6 cm long and the body is 0.45 cm in depth (Schultze, 1994). The hypotype is slightly larger, 5.2 cm long and 0.7 cm in depth (Schultze, 1994).

The left upper tooth plate of *P. parvulus,* although not well preserved, displays the characters of many other small lungfish tooth plates. The few surviving cusps are separate and still distinct, and wear appears to be slight. None of the labial or the most medial cusps can be reliably assessed as the ridge tips and the medial face of the tooth plate are broken. There is no trace of the formation of additional dental tissues, represented by secondary denteons (punctations) that cause thickening of dental material between the ridges of the tooth plate. The right upper tooth plate, represented by three whole cusps of the first ridge, reveals that the enamel covering of the cusps reached the tips in this specimen. There is no sign of wear on the cusps. Squamation in both specimens is complete, extending as far as the head, and most of the calvarial, palatal, and mandibular bones appear to be present.

The macerated condition of the head in both specimens means that it is not possible to describe with any accuracy the pattern of the dermal skull roof or the cheek region of the holotype or the hypotype. Most of the bones have lost their original relationships, and the few that remain close together suggest one pattern in the holotype and another in the hypotype (Schultze, 1994). Articulation may not have been complete in either specimen.

As in both specimens of *P. parvulus,* a full set of squamation is present in *N. forsteri* from stage 53 onward (Kemp, 1982). At stage 53 in *N. forsteri* the larger calvarial bones have begun to form and to ossify but are not yet articulated with each other. The smaller calvarial bones have not appeared. Jaws are represented at stage 53 by well-ossified prearticular, articular, and pterygopalatine bones, and the parasphenoid, ceratohyal, and shoulder girdle are also mineralized. Articulations of palatal, mandibular, and shoulder girdle bones are forming. The vomer, positioned on the rostral cartilage of the chondrocranium, is also ossified, but never forms an articulation with any bone. At stage 55, most of the calvarial bones are present and anterior calvarial articulations have begun to form, although these are still incomplete, as is the process of ossification of the bones. The descending process of the anterior mediolateral bone, JLM in the nomenclature of Kemp (1992a), and the ascending process of the pterygopalatine bone are not yet fully articulated. The palate and lower jaw, with associated tooth plates, and the shoulder girdle are well ossified and firmly articulated.

The tooth plates of *N. forsteri* at stages 54–56 parallel exactly the structure of the smaller *M. stenodonta* and *Sagenodus* tooth plates, of comparable size, and the upper tooth plates of *P. parvulus,* as far as can be discerned (Fig. 2, 4). The cusps are clearly demarcated, and increase in size from the oldest, first-formed parts of the tooth plate to the youngest labial fringes. Each ridge has no more than six cusps, and each cusp shows little or no wear, even the medial cusps. In some specimens, a complete coat of enamel extends to the tip. Cusps can be

Table 3.—*Data matrix for juvenile dipnoans, generic characters. Characters are listed in Appendix.*

Genus	Character State			
Sagenodus	00000	00000	00000	000
Neoceratodus	11100	01000	01111	111
Monongahela	00111	00011	11111	111
Palaeophichthys	????1	?1?0?	01?1?	???

distinguished all the way to the mediolingual edge. There is no development of secondary denteons or thickening between the primary ridges. This appears much later, along with removal of cusps through wear, and the appearance of additional ridges and destructive removal of enamel and dentine from the mediolingual face of the tooth plate (Kemp, 1977, 1979).

All of the specimens of *M. stenodonta* fall within a narrow size range (Table 2). The smaller specimens, those comparable in size to *P. parvulus,* have characters consistent with those of other juvenile dipnoans (Fig. 4). Cusps are clearly demarcated, and grade in size from the smallest medial cusps to the largest labial cusps that have fused recently to the underlying bone base. The cusps are few in number, sharp, and show little wear. Where wear is present, it is restricted to the medial cusps. Secondary denteons have not yet appeared, and the ridges are cusped to the mediolingual face. These characters are evident in specimens of *S.* cf. *S. periprion* as well. Specimens of this species are slightly larger than those of *M. stenodonta,* but still have sharp conical cusps on each ridge, and all of the cusps are unworn. Posterior ridges with only one or two cusps indicate that the tooth plate was still growing actively at the time of death (Fig. 4E, F).

In larger *M. stenodonta* tooth plates, but not in *Sagenodus,* medial cusps show considerable wear, and labial cusps are still sharp. However, in both forms, none of the tooth plates show any development of secondary denteons, or thickening of tooth plate material, between the primary ridges of the tooth plate. The range of specimens available extends to material much larger than *P. parvulus.*

Angles between the Ridges.—The angles listed by Schultze (1994) as specific diagnostic characters of *P. parvulus* are 40° between ridges 1 and 2 and 28° between ridges 2 and 3. He does not give an angle for ridges 3 and 4. Angles measured on the scan by the methods used for other small lungfish in this work are 35°, 24°, 20°, and 18°, respectively (Table 2). Angles between the ridges of pterygopalatine tooth plates in *N. forsteri* and *M. stenodonta* are of comparable size (Table 2), and become progressively smaller in the posterior regions of the tooth plate, as in *P. parvulus.* Angles between ridges of *N. forsteri* are 51.6°, 35.7°, and 24.7° for ridges 1–2, 2–3, and 3–4 respectively (Table 2). Corresponding angles in *M. stenodonta* are 40.4°, 40.2°, and 31.2° (Table 2). Angles between the ridges of *S.* cf. *S. periprion* are much smaller and closer in size, 10.7°, 16.2°, 14.7°, and 20.2° for ridges 1–2, 2–3, 3–4, and 4–5 (Table 2).

Character Determination.—Character states for the species considered in this paper are given in the data matrix (Table 3). The reconstruction of *P. parvulus* that is closest to the interpretation of Schultze (1994) has been used for the determination of characters.

Cladistic analysis of these genera has not been performed because much of the data available for *N. forsteri, M. stenodonta,* and *S.* cf. *S. periprion* cannot be predicted or assumed for *P. parvulus.* The relevant parts of the specimen are missing, reducing the useful information to six characters (Table 3). An estimation

of phylogenetic relationships among the taxa considered here, based on the six characters and using *Sagenodus* as the outgroup, suggests that *P. parvulus* and *M. stenodonta* are both more derived than *N. forsteri,* but share few derived characters.

DISCUSSION

Ontogeny of *N. forsteri* is not always seen as relevant to the study of fossil dipnoan tooth plates (Campbell and Barwick, 1995), and it is certainly true that *N. forsteri* is not as closely related to *Monongahela* and *Gnathorhiza* as are the other Recent lungfishes, *Lepidosiren paradoxa* from South America, and species of *Protopterus* from Africa (Lund, 1970, 1973). Ontogeny of *N. forsteri* tooth plates is, however, better known than it is in lepidosirenids (Kerr, 1903, 1910; Kemp, 1977, 1979, 1992*b*, 1995*b*), and growth stages of *M. stenodonta* are comparable (Lund, 1970). Lepidosirenid lungfish also have tooth plates that are derived from the fusion of isolated cusps in radiating ridges, a form of development common in many lungfish, including *N. forsteri* (Kemp, 1995*b*). At the present state of our knowledge of lepidosirenid ontogeny, comparisons are limited to *N. forsteri,* and the juvenile tooth plates of this species are less different to those of *M. stenodonta* than they first appear to be. The ontogeny of *N. forsteri* is relevant to the study of fossil dipnoans, particularly the more derived of post-Paleozoic genera.

Small size does not necessarily mean that a fossil must have been or have come from a juvenile animal. It is not possible to be certain that a fossil known from limited material of minute size represents a juvenile animal or perhaps an adult, because a representative sample of life stages is rarely present. Criteria derived from comparison with living representatives of the group can be used instead to assess the biological age of a fossil at death. These can be drawn from body and head measurements, squamation, degree of development of skull bones, formation of firm articulations between skull bones, and a number of tooth plate characters, like the form of the cusps, their enamel cover, and the development of secondary denteons.

All of the fossil tooth plates examined for this study have the characteristics that define young *N. forsteri* of known stage of development and known biological age. Based on these criteria, it can be shown that *P. parvulus* and *M. stenodonta* specimens are the remains of juvenile fishes, and as such can be compared with the tooth plates of juvenile specimens of the Recent lungfish and with other juvenile fossil dipnoans, like specimens of *S.* cf. *S. periprion.* The specimens referred to *P. parvulus* and *M. stenodonta* are not as easily comparable with the tooth plates of adult lungfishes, including those of *Gnathorhiza.*

It is possible to discriminate species on juvenile material in a bradytelic group like lungfish, even if the only useful parts are tooth plates, provided that characters are chosen with care. This unfortunately leaves a restricted list. Many of the tooth plate characters used for discrimination among adult lungfish (Kemp, 1992*a,* 1993*a*), like the form of the prearticular sulcus, have not yet developed fully in hatchlings and juveniles. Other characters, like the origin of ridges, differ in juveniles and adults of the same species. In young *N. forsteri,* the three or four ridges are medial in origin, but in adults, with six or seven ridges, they are anterior in origin. (A medial origin for adult *N. forsteri,* stated in Kemp, 1993*a*:table 1, is a mistake.) Shapes in the jaw bones are not always useful. The form of the

jaw bone behind the tooth plate is often not preserved, and shows little variation. Most dipnoans have strong articular or quadrate processes on the prearticular and pterygopalatine bones, and the shapes are often similar. The same applies to the relationship between the first ridge and the symphysis. This is almost always parasymphyseal. Ridge length is not a reliable character either. In very young tooth plates, with only three or four cusps in a ridge, the addition of a single new cusp can make a large difference to the total length of the ridge.

The only points of comparison between *P. parvulus* and *M. stenodonta* are the preserved first ridge of the right pterygopalatine tooth plate and the imperfect impression of the left pterygopalatine tooth plate in the holotype of *P. parvulus,* and the large number of specimens of *M. stenodonta* tooth plates known. Generic identity has to be demonstrated on the upper tooth plates, as the only lower tooth plate present is too poorly preserved to distinguish any diagnostic characters. Examination of the few reliable characters indicates that separation of the two genera is appropriate, even using the reconstruction that is closest to the interpretation of Schultze (1994). Using any of the other possible reconstructions of the left pterygopalatine tooth plate of *P. parvulus* only serves to increase the differences between *P. parvulus* and *M. stenodonta.* This conclusion is, however, provisional, because reliable data are scarce.

Skull bones are not consistent between the holotype and hypotype of *P. parvulus,* and, apart from indicating that *P. parvulus* cannot be a gnathorhizid, have no impact on the question of synonymy with *M. stenodonta.* Species of *Gnathorhiza* and related genera all have a double C bone in the medial series (Berman, 1968, 1976, 1979; Olson and Daly, 1972; Kemp, 1993*b*). The few discernible postcranial features of *P. parvulus* are not particularly gnathorhizid in character. Juvenile gnathorhizids have been described as having a rounded eel-like body form, with a short, blunt tail and a head one-fifth of the body length (Dalquest, 1968). Using skull and body-form characters, *Palaeophichthys* is not a gnathorhizid.

There are at least six possible reconstructions of the upper tooth plate of *P. parvulus.* Each interpretation suggests different affinities for *P. parvulus.* It is possible that the tooth plate has five ridges, relating the hatchling to *Sagenodus* or to one of the undescribed species of dipnoan from either locality. It can also be interpreted as having three ridges. A small number of radiating ridges in a young fossil tooth plate, with cusps entirely covered in enamel and no secondary denteons present, is not uncommon. Equivalent characters are found in young *Megapleuron zangleri* (Schultze, 1977), a species occurring in Pennsylvanian deposits in North America, and in many other post-Paleozoic dipnoans, including *N. forsteri.* A third possibility is that it has four ridges, with the fourth ridge originating midway down the third. Joining of the fourth ridge on to the third lateral to the apex of the tooth plate is found in young *Gnathorhiza* as well as in *M. stenodonta,* a large proportion of small *N. forsteri,* and doubtless other dipnoans. Since the apex is missing, all the ridges, three, four, or five, could meet in a point, as is common in young *N. forsteri* and in *M. stenodonta,* or join a line or curve as in young *Sagenodus.*

Schultze (1994) has given a specific diagnosis of *P. parvulus* based entirely on the angles between ridges, and his measurements fall within the range of angles found in *M. stenodonta* (Lund, 1970, 1973; Schultze, 1994). Angles between the ridges are only valid as taxonomic determinants if based on a large statistical sample (Vorobyeva, 1967; Kemp, 1977). They should be measured on well-pre-

served and preferably original tooth plates, and care should be taken to distinguish the growth angles from the wear angles. Angles also vary among individuals of one species and between juvenile and adult specimens of the same species (Kemp, 1977). Variability is obvious in all of the species measured on tooth plates in this study. Because a diagnosis is intended to characterize a species or a genus to the exclusion of others, beyond reasonable doubt, angles do not have any validity measured on a cast of a single juvenile tooth plate.

Vomerine tooth plates of most post-Paleozoic dipnoans resemble a single ridge of the more complex prearticular and pterygopalatine tooth plates, and have cusps at the actively growing labial end. This is true even in large, old specimens. If the structure identified as a vomerine tooth plate by Schultze (1994) is a vomerine tooth plate, the lack of cusps is, firstly, most unusual and, secondly, a significant point of difference with *M. stenodonta*. This species has numerous minute cusps on the vomerine tooth plate (Lund, 1970).

The deposit from which *P. parvulus* was obtained contains at least three other species of lungfish (Lund, 1975, 1976; Hook and Baird, 1986, 1993). One of these, *Conchopoma,* differs fundamentally in skull and tooth-plate characters from most other post-Paleozoic dipnoans (Hook and Baird, 1993), and can be excluded as a genus that is close to *Monongahela* or *Palaeophichthys*. The deposit from which *Monongahela* came also contains other species of lungfish (Lund, 1970, 1973, 1975, 1976). None of these dipnoans is perfectly preserved and none can be characterized completely. *Palaeophichthys* is best classified as incertae sedis, a monotypic genus of uncertain affinities based on incomplete juvenile material. It is unlikely to be closely related to *Gnathorhiza* because it has an unpaired median C bone in the dermal skull roof (Schultze, 1994). *Monongahela* is a genus with close relationships to *Gnathorhiza,* and is known from an extensive series of dental material and attached jaws (Lund, 1970, 1973). Our knowledge of all of these species is incomplete, and *Monongahela* should not be regarded as a junior synonym of *Palaeophichthys*. Additional studies of all of these lungfishes are needed to decide questions of generic status.

LITERATURE CITED

BARDACK, D. 1979. Fishes of the Mazon Creek fauna. Pp. 501–528, *in* Mazon Creek Fossils (M. H. Nitecki, ed.). Academic Press, New York, New York.

BERMAN, D. S. 1968. Lungfish from the Lueders Formation (Lower Permian, Texas) and the *Gnathorhiza*–lepidosirenid ancestry questioned. Journal of Paleontology, 42:827–835.

———. 1976. Cranial morphology of the Lower Permian lungfish *Gnathorhiza* (Osteichthyes: Dipnoi). Journal of Paleontology, 50:1020–1033.

———. 1979. *Gnathorhiza bothrotretata* (Osteichthyes: Dipnoi) from the Lower Permian Abo Formation of New Mexico. Annals of Carnegie Museum, 48:211–230.

CAMPBELL, K. S. W., AND R. E. BARWICK. 1995. The primitive Dipnoan dental plate. Journal of Vertebrate Paleontology, 15:13–27.

CARROLL, R. L. 1988. Vertebrate Paleontology and Evolution. Freeman and Company, New York, New York.

DALQUEST, W. W. 1968. Lungfishes from the Permian of Texas. Copeia, 1968:194–197.

EASTMAN, C. R. 1908. Devonian fishes of Iowa. Iowa Geological Survey 18, Annual Report, 1907: 29–386.

———. 1917. Fossil fishes in the collection of the United States National Museum. U. S. National Museum Proceedings, 52:235–304.

HOOK, R. W., AND D. BAIRD. 1986. The Diamond Coal Mine of Linton, Ohio, and its Pennsylvanian-age vertebrates. Journal of Vertebrate Paleontology, 6:174–190.

———. 1993. A new fish and tetrapod assemblage in the Allegheny Group (Late Westphalian, Upper Carboniferous) of eastern Ohio, USA. Pp. 143–154, in New Results on Permo–Carboniferous Faunas (U. Heidke, ed.). Pollichia-Buch 29, Pfalzmuseum für Naturkunde, Bad Dürkheim, Germany.

JESSEN, H. 1973. Weitere Fischreste aus dem Oberen Plattenkalk der Bergisch–Gladbach–Paffrather Mulde (Oberdevon, Rheinisches Schiefergebirge). Palaeontographica (Abteilung A), 143:159–187.

KEMP, A. 1977. The pattern of tooth plate formation in the Australian lungfish, *Neoceratodus forsteri* (Krefft). Zoological Journal of the Linnean Society, London, 60:223–258.

———. 1979. The histology of tooth plate formation in the Australian lungfish, *Neoceratodus forsteri* (Krefft). Zoological Journal of the Linnean Society, London, 66:251–287.

———. 1982. The embryological development of the Queensland lungfish, *Neoceratodus forsteri* (Krefft). Memoirs of the Queensland Museum, 20:553–597.

———. 1991a. Australian Mesozoic and Cainozoic lungfish. Pp. 465–498, in Vertebrate Palaeontology of Australasia (P. Vickers-Rich, J. M. Monaghan, R. F. Baird, and T. Rich, eds.). Pioneer Design Studio, Melbourne, Australia.

———. 1991b. Palaeopathology and lungfish tooth plates. Pp. 441–464, in Early Vertebrates and Related Problems of Evolutionary Biology (M.-M. Chang, Y.-H Lui, and G.-R. Zhong, eds.). Science Press, Beijing, People's Republic of China.

———. 1992a. New neoceratodont cranial remains from the Late Oligocene–Middle Miocene of northern Australia with comments on generic characters for Cenozoic lungfish. Journal of Vertebrate Paleontology, 12:284–293.

———. 1992b. Ultrastructure of the developing dentition in the Australian lungfish, *Neoceratodus forsteri* (Krefft). Pp. 11–33, in Structure, Function and Evolution of Teeth (P. Smith and E. Tchernov, eds.). Freund Publishing House, Tel Aviv, Israel.

———. 1993a. *Ceratodus diutinus*, a new fossil ceratodont from Cretaceous and Tertiary deposits in Australia. Journal of Paleontology, 67:883–886.

———. 1993b. Problematic fossil dipnoans from Australia. New Mexico Museum of Natural History and Science Bulletin, 3:223–227.

———. 1995a. Complex dentines in fossil lungfish tooth plates. Pp. 210–215, in Proceedings of the Tenth International Symposium on Dental Morphology (R. J. Radlanzki, H. Renz, eds.). "M" Marketing Services, Berlin, Germany.

———. 1995b. Marginal tooth-bearing bones in the lower jaw of the Recent Australian lungfish, *Neoceratodus forsteri*, (Osteichthyes:Dipnoi). Journal of Morphology, 225:1–11.

KERR, J. G. 1903. The development of *Lepidosiren paradoxa*. III. Development of the skin and its derivatives. Quarterly Journal of Microscopical Science, 46:417–459.

———. 1910. On certain features in the development of the alimentary canal in *Lepidosiren* and *Protopterus*. Quarterly Journal of Microscopical Science, 54:483–518.

LISON, L. 1941. Recherches sur la structure et l'histogenese des dents des poissons dipneustes. Archives de Biologie (Paris), 52:279–320.

LUND, R. 1970. Fossil fishes from southwestern Pennsylvania. Part I. Fishes from the Duquesne limestones (Conemaugh, Pennsylvanian). Annals of Carnegie Museum, 41:231–261.

———. 1973. Fossil fishes from southwestern Pennsylvania. Part II. *Monongahela dunkardensis*, new species, (Dipnoi: Lepidosirenidae) from the Dunkard group. Annals of Carnegie Museum, 44:71–101.

———. 1975. Vertebrate fossil zonation and correlation of the Dunkard Basin. Pp. 171–182, in The Age of the Dunkard, Proceedings of the First I. C. White Memorial Symposium (J. A. Barlow, ed.). West Virginia Geological and Economic Survey, Morgantown, West Virginia.

———. 1976. General geology and vertebrate biostratigraphy of the Dunkard Basin. Pp. 225–239,

in The Continental Permian in Central, West and South Europe (H. Falke, ed.). D. Reidel Publishing Company, Dordrecht, Holland.

LUND, R., P. BARTHOLOMEW, AND A. KEMP. 1992. The composition of the dental hard tissues of fishes. Pp. 35–71, *in* Structure, Function and Evolution of Teeth (P. Smith and E. Tchernov, eds.). Freund Publishing House, Tel Aviv, Israel.

MAPLES, R. AND H.-P. SCHULTZE. 1989. Preliminary comparison of the Pennsylvanian assemblages of Hamilton, Kansas, with marine and non-marine contemporaneous assemblages. Pp. 253–273 *in* Regional Geology and Paleontology of Upper Palaeozoic Hamilton Quarry Area in Southeastern Kansas (G. Mapes and R. Mapes, eds.). Kansas Geological Survey Guidebook, Series 6.

OLSON, E. C., AND E. DALY. 1972. Notes on *Gnathorhiza* (Osteichthyes: Dipnoi). Journal of Paleontology, 46:371–376.

ROMER, A. S. 1966. Vertebrate Paleontology. Third Edition. The University of Chicago Press, Chicago, Illinois.

SCHEVILL, W. E. 1932. Fossil types of fishes, amphibians, reptiles and birds in the Museum of Comparative Zoology. Bulletin of the Museum of Comparative Zoology, 74:57–105.

SCHULTZE, H.-P. 1977. *Megapleuron zangleri,* a new dipnoan from the Pennsylvanian, Illinois. Fieldiana: Geology, 33:375–396.

———. 1992. Dipnoi. Pp. 1–464 *in* Fossilium Catalogus, Volume 131 (F. Westphal, ed.). Kugler Publications, Amsterdam, The Netherlands.

———. 1994. *Palaeophichthys parvulus* Eastman, 1908, a gnathorhizid dipnoan from the Middle Pennsylvanian of Illinois, USA. Annals of Carnegie Museum, 63:105–113.

SCHULTZE, H.-P., AND C. R. MARSHALL. 1993. Contrasting the use of functional complexes and isolated characters in lungfish evolution. Memoirs of the Association of Australasian Palaeontologists, 15: 211–224.

VOROBYEVA, E. I. 1967. A Triassic ceratod from South Fergana and remarks on the systematics and phylogeny of ceratodontids. Paleontologiskii Zhurnal, 1967:102–111 (translated Paleontological Journal, 1967:80–87).

VOROBYEVA, E. I., AND D. V. OBRUCHEV. 1964. Subclass Sarcopterygii. Pp. 268–321, *in* Osnovy Paleontologii, Volume Two. Agnatha, Pisces (Y. A. Orlov, ed.). Izdatelstvo "NAUKA" SSSR, Moscow, USSR. (In Russian)

APPENDIX

Character Descriptions

The characters in the following list were used to assess the Recent and fossil tooth plates from juvenile dipnoans. Characters that could be determined on *Palaeophichthys parvulus,* marked with an asterisk, were too few to permit a cladistic analysis of the groups. Primitive states for each character are coded as "0" and determined from the condition of the outgroup, *Sagenodus*. The derived state is coded as "1."

1. Upper symphysis linear (0), upper symphysis not linear (1).
2. Lower symphysis oval (0), lower symphysis not oval (1).
3. Ascending pterygopalatine process absent (0), ascending pterygopalatine process present (1).
4. Petrodentine absent (0), petrodentine present (1).
*5. Ridge 1 (upper) curved (0), ridge 1 (upper) straight (1).
6. Ridge 1 (lower) straight (0), ridge 1 (lower) curved (1).
*7. Posterior ridges (upper) curved (0), posterior ridges (upper) straight (1).
8. Posterior ridges (lower) straight (0), posterior ridges (lower) curved (1).
*9. Cusps of ridge 1 (upper) show slight lateral compression (0), cusps of ridge 1 (upper) show strong lateral compression (1).
10. Cusps of ridge 1 (lower) show slight lateral compression (0), cusps of ridge 1 (lower) show strong lateral compression (1).
*11. Cusps of posterior ridges show slight lateral compression (0), cusps of posterior ridges show strong lateral compression (1).
*12. Five ridges or more in upper jaw (0), fewer than five ridges in upper jaw (1).

* Data available from *P. parvulus,* using the interpretation of Schultze (1994) and the reconstruction of Figure 2D.

13. Four ridges or more in lower jaw (0), fewer than four ridges in lower jaw (1).
*14. Ridge 4 (upper) begins level with ridge 3 (0), ridge 4 (upper) begins midway down ridge 3 (1).
15. Pterygopalatine bone extends beyond dentine ridges (0), pterygopalatine bone follows line of dentine ridges (1).
16. Prearticular bone extends beyond dentine ridges (0), prearticular bone follows line of dentine ridges (1).
17. Upper ridges radiate from a mediolingual line (0), upper ridges radiate from a mediolingual point (1).
18. Lower ridges radiate from a mediolingual line (0), lower ridges radiate from a mediolingual point (1).